Canopy Transpiration in a Chronosequence of Central Siberian Pine Forests

Zimmermann Reiner [1,3], Schulze Ernst - Detlef [2], Wirth Christian [2], Schulze Ernst - Eckart [2], McDonald Kyle C [3], Vygodskaya Natascha N [4], Ziegler Waldemar [2, 5]

(1) University of Bayreuth, Dept. of Plant Ecology, Universitätsstrasse 30, D-95440 Bayreuth, Germany

(2) Max Planck Institute for Biogeochemistry, Post box 100164, D-07743 Jena, Germany

(3) Jet Propulsion Laboratory, Terrestrial Science Research Element, California Institute of Technology, Pasadena 91109, California, USA

(4) Sukachev Laboratory of the Institute of Evolution and Ecology Problems, Russian Academy of Sciences, Lininsky Prospect 33, 117071 Moscow, Russia

(5) Department of Biophysics and Chemical Physics, Comenius University, Mlynska Dolina F1, SK-84215, Bratislava, Slovakia

Keywords:

Transpiration, canopy conductance, microclimate, xylem flux, *Pinus sylvestris*, Siberia.

Corresponding author:

Reiner Zimmermann, University of Bayreuth, Dept. of Plant Ecology, Universitätsstrasse 30, D-95440 Bayreuth, Germany. Phone: ++ 49 - 921 - 552573 Fax: ++ 49 - 921 - 555799

Email: reiner.zimmermann@bitoek.uni-bayreuth.de

Running title:

Canopy Transpiration in Siberian Pine Forests

Abstract

Tree transpiration was measured in 28, 67, 204 and 383 - year old uniform stands and in a multi-cohort stand (140 to 430 years) of *Pinus sylvestris ssp. sibirica* Lebed. in Central Siberia during August of 1995. Transpiration of three trees was monitored for two years in a 130 - year stand. Stand leaf area index was low (LAI 0.6 at 28 - years and ; LAI 1.6 for > 67 - years). Stand xylem area at 1.3 m height increased from 4 $cm^2\ m^{-2}$ (28 - year) to 11.5 $cm^2\ m^{-2}$ (67 - year) and decreased again to 7 $cm^2\ m^{-2}$ in old stands. Aboveground living biomass increased from 1.5 kg dry weight m^{-2} (28 - year) to 14 kg dry weight m^{-2} (383 - year). Maxima of sap flux density (60 g $m^{-2}\ s^{-1}$) and canopy transpiration (1.5 mm day^{-1}) were reached in the 67 - year stand. Maximum canopy transpiration averaged for all age classes did not exceed 0.85 mm day^{-1}. Canopy transpiration (E) was not correlated with LAI but related to stand sapwood area SA (E=-0.02+1.15 SA R^2) as a function of stand density and tree sapwood area. Day-to-day variation of tree transpiration in summer was dependent on net radiation, vapor pressure deficit, and soil water stress. Tree-to-tree variation of xylem flux was small but increased with heterogeneity in canopy structure. Maximum rates of xylem flux density followed the course of net radiation from mid April when a constant level of maximum rates was reached until mid September when low temperatures and light strongly reduced flux density. Tree canopy transpiration in a 204 - year old stand was 49 mm from April 21 to October 20 (182 days). If evaporation from the forest floor and from wet canopies is included, forest evaporation uses 61 % of the summer rainfall of 297 mm.

Introduction

Eddy correlation measurements above pine forests of Siberia indicated, that in the continental climate of Siberia the ecosystem transpiration almost balances precipitation. Kelliher et al. (1998) estimated that only about 10 % of the 300 mm summer rainfall was seeping into the ground water table. These predictions were based on measurements in old grown pine forest of very low leaf area index during mid-summer. However, scaling up of eddy correlation measurements in boreal forests in order to estimate water exchange processes at a regional scale may be problematic because forest stands regenerate after fire (Wirth et al., 1998), and result in a mosaic of small scale forest patches (0.1 to > 10 ha) differing in age. For predictions of the regional water balance it remains unknown, to what extend the water balance varies with stand age and which are the structural components that determine canopy water loss. We hypothesize, that canopy water loss is a function of sapwood area and stand density which is modified by climate. However, *a priori* there is no way to predict which age class or canopy structure will reach highest transpiration rates in a boreal forest.

This paper aims at quantifying canopy water loss in a chronosequence of pristine Siberian pine stands which regenerated naturally after fire and at determining the relations between canopy transpiration and structural components (stand age, leaf area index, stand density and sapwood area) and climatic factors.

Materials and Methods

Site description

Scots pine (*Pinus sylvestris* L.) has the widest natural distribution range of all conifers, extending over more than 160 ° longitude from the European Atlantic coast almost to the Pacific (Walter and Breckle, 1994). Almost 37 % of the forested area and 31 % of the West Siberian growing stock timber is based on this coniferous species (Shvidenko and Nielsson,1994). Pine is a species with a high demand for light. It is well adapted to frost, drought, low nutrient availability and in a mature stage to ground fires. In Siberia, pine stands dominate forests between the Ural mountains and the Jenisei river, where forests and *sphagnum* bogs occur in a mosaic landscape on alluvial sand dunes which were deposited during the early holocene when the arctic ice shield retreated.

Measurements were made in pure and even aged stands of 28, 67, 204, and 383 years and in a senescent stand consisting of 140 to 430 year old trees with DBH varying from 9.2 cm to 49.4 cm (Tab. 1). These stands were located in the geographic center of Siberia at 60° 43' North, 89° 09' East, west of the Jenisei river and 40 km SW of the village of Zotino (61° N, 89 ° E, 160 m a.s.l.).

Following a dense regeneration after fire (Fig. 1) canopies reach 4 to 5 m height after 28 years. Stand density remains high up to the pole stage (67 -

year old stand of 10 m height) when self-thinning and ground fires, which occur in average every 22 years (Wirth et al., 1998), reduce stand density. The pine stands of this study reached heights of 15 to 20 m after >200 years. Senescent stands (>400 years) are rare, since major fires occur about every 200 years which initiate establishement of a new forest generation.

Stem diameter at breast height (DBH) and aboveground stand biomass increased with stand age (Tab. 1) while basal area and leaf area index remained almost constant from age 67 to 380 at decreasing stem density. Only sapwood area did not follow this trend but reached a maximum at age 67 at high tree density.

Xylem flux measurements

Xylem flux was measured continuously with a thermal method (Granier 1985). Sap flux density in the youngest part of the hydroactive xylem was derived from continuous measurements of heat dissipation in the stem xylem at 0.5 m (small trees) to 1.8 m height above the ground. With constant thermal energy dissipation (0.2 Watt, sensor length 20 mm at 2 mm diameter) the apparent temperature difference between the stem tissue 15 cm below the heated probe was measured. Temperature difference was measured with two inversely connected 0.2 mm diameter Cu-Constantane thermocouples and monitored every 30 seconds. A ten minute mean was stored on a logger for each sensor.

The sensor setup was covered with a radiation shield to avoid radiative thermal load on the sensors. In each stand, 6 to 12 trees were instrumented, representing the range of DBH of this stand. The xylem flux sensor insertion was at a randomly choosen exposition on the trunk to account for variations in sap flow density, related to variations among trees and exposure.

Whole tree transpiration was estimated by multiplying the average xylem flux density from all trees in each stand by the total stand xylem area, which was determined from tree discs of representative subsamples in all age classes. The xylem depth was clearly visible on tree discs and in most cases symmetrically shaped. A regression was established for each stand to predict xylem area from DBH (x = Basal area without bark [m^2]; y = Xylem area [m^2]; 28-year old: tree cross section equals xylem area; 67-year old: y = 0,652 x R^2=0,942 n=5; 138-year old: y = 0,382 x R^2=0,238 n=4 (extensive fire damage on discs); 204-year old: y = 0,379 R^2 = 0,911 n=5; 383-year old: y = 0,284 R^2 = 0,910 n=5; Multi-cohort 140 to 430-year old: y = 0,3919 R^2=0,746 n=4). Canopy conductance was calculated from measured tree transpiration and the VPD as measured in a forest clearing. Needle temperatures were assumed to be close to air temperature due to their small volume.

Power for the sensor setup at each site was provided by lead-acid batteries (12 VDC, 110 Ah). Batteries were either recharged by gasoline powered generator or by solar panels (MSX-30, Solarex, USA) with charge controler (M-8, Bobier Electronics, USA). Microclimatic and xylem flux density sensors were automatically logged on a data logger at each site (DL-2 with LAC-1 in double ended mode, Delta-T Devices, England). Data were downloaded with a laptop PC and processed using Dataman (Ce Huang, Duke University, USA), Sigmaplot 4.0 (Jandel Inc. USA), SPSS (SPSS Inc., USA), and Excel 4.0 (Microsoft, USA).

Micrometeorological measurements

Site climate was measured on a flat, sandy area with scattered old trees near the 383 year old stand: Air temperature (6 m above ground) with a linearized thermistor and relative humidity with a capacitive sensor of a high recovery rate after water vapor saturation (HMP-35C, Campbell Scientific Inc., Logan USA). Air temperature and relative humidity readings were checked against a sling psychrometer (Baccarach, USA). Photosynthetically active radiation was measured with a PAR sensor (LI-190, LI-COR, USA), solar irradiance with a pyranometer (LI-200, LI-COR, USA), and precipitation with a dynamic tipping bucket rain gauge of 0.1 mm resolution (TE525, Campbell Sci. Inc., USA). The daily total of the dynamic rain gauge was checked against a wedge type rain collector (Truecheck, USA) next to it.

At each stand, the air and soil temperatures were measured with small thermistors (M841/S1/3K, Siemens, Germany) at 2 m and 0.1 m above the ground (both with metal radiation shield), in the litter layer (approx. - 0.01 m depth), and in the mineral soil (-0.1 m, -0.25 m, -0.5 m depth). Soil moisture

was monitored with cylindrical soil moisture blocks (Mod. 227 Delmhorst Co., USA) in the mineral soil at 0.1 m, 0.25 m, and 0.5 m depth.

Experimental design

For the stand comparison ranging from 28 years to the senescent stage, six to twelve trees were monitored with xylem sensors during an intensive field campaign in July 1995. For the seasonal trend in transpiration, long-term measurements were carried out in a 130 year old stand at the site of Bor Island (Goldammer et al. 1996), using 3 representative trees only, due to the limitations given by the solar power supply and battery backup. The measurements were interrupted twice. In November 1995 the lead battery froze up and did not recover. The datalogger setup was reinstalled in a sealed box at 1 m below ground during a visit in April 1996 and logged data until June 1997 when a bear uncovered the instruments.

Results

Stand comparison

The intensive measurement campaign took place during a ten day period of dry and sunny weather between two major summer rainstorms, a climatic situation which is typical for the central Siberian summer. Following a nocturnal thunderstorm with 19 mm precipitation on day 215 (Fig. 2) the daily mean temperature decreased from 20 °C to 12 °C, but increased again to above 20 °C within five days. Maximum air temperature reached about 33 °C and daily VPD reached 3.1 kPa shortly before the second rain storm on day 225.

Fig. 3 shows the daily course of sap flow density of individual trees for each plot on a day in the middle of the dry period when VPD had reached 2.7 kPa at 20 °C air temperature. Topsoil temperatures reached 25 °C in stands with relatively closed canopy and increased to 35 °C in open stands. Within each plot diurnal flow patterns were uniform and independent of tree size. Only suppressed and damaged trees had lower flux rates while emergent trees tended to show higher rates than the canopy average.

The daily course of sap flow density was distinct for each stand age class. The 28 - year old stand reached the highest sap flux density as compared to all other plots, but rates decreased throughout the day inversely to VPD. This pattern changed with stand age in a way that the morning peak of transpiration

became lower, and the diurnal course changed from a morning peak towards a curve showing a morning and an afternoon peak (204 year old stand) or it remained at constant sap flux rates. The two peaked diurnal course indicates a stomatal response to low air humidity (Schulze et al. 1973; Vygodskaya et al., 1997) while the tree response to plant water stress is less clear. In the young stand with mainly surface roots the lack of recovery of sap flow rates in the afternoon may indicate depletion of water in the top soil surface layer, water content seems to recover during the night. Increasing stand age and a deeper soil rooting depth seem to stabilize the plant water status at a lower rate and trees responded less to VPD. Also, with increasing stand age, the variation in sap flow rates between trees in the same stand increased due to the individual history of crown and stem damage (Wirth et al., 1998).

Canopy transpiration and canopy conductance were calculated from the average sap flux of measured trees (n=7 to 9 per stand) and the total stand sap wood area (Fig. 4). The measurements took place in a period of warm and dry weather between two major rain events. Since the water holding capacity of the sandy soil was low, all stands went through a drought cycle. Canopy conductance was high after rainfall and decreased continuously in all age classes to a lower and constant level within 4 to 5 days. However, since VPD increased as a result of higher air temperatures canopy transpiration remained at a constant level of about 0.85 mm d^{-1} for most sites. Only the 67 year old stand wich had a higher sapwood area transpired about twice as much. The senescent site reached about half the transpiration rate as compared to the average. The average canopy transpiration measured by thermal flux technique was not significantly different from the canopy rates of transpiration (0.57 ± 0.23 mm d^{-1}) as measured by above canopy eddy correlation (1.25 ± 0.36 mm d^{-1}) minus soil evaporation (0.72 ± 0.31 mm d^{-1}) in the same area in 1996 by Kelliher et al. (1998).

The response of the canopy to the morning increase in VPD (Fig. 5) showed pronounced stomatal closure at a high level of conductance in the 67 - year old pole stand which even lead to a decreased transpiration at high VPD (Nonami et al., 1990). In all other stands the change in conductance did not significantly reduce the water loss by transpiration. In all cases canopy conductance recovered during the afternoon under conditions of reduced VPD and light while transpiration remained low (data not shown).

Canopy transpiration was neither related to LAI nor to basal area. However, canopy transpiration was closely correlated with stand sapwood area ($E= -0.02 + 1.15\ SA$, $r=0.96$). Stand sapwood area is determined by two counteracting processes, the exponential decrease of stand density with tree age (Fig. 7) and an almost linear increase of sapwood area per tree with stand age. This resulted in a maximum sapwood area in the 67 - year old dense pole stand before self- thinning becomes prevalent. Obviously the high stand sapwood area results in a close coupling between root and shoot at the same time when deeper rooting starts to improve the plant water status (Grace 1993).

Annual course of canopy transpiration

The seasonal change of transpiration was measured on three trees due to restrictions in power supply and storage capacity of the data logger at the remote location. Frost and bear damage interrupted the measurements twice. Thus, the seasonal course shown in Fig. 7 results from combined measurements of the years 1996 (days 202-366) and 1997 (days 1-163).

During summer of 1995, which was a relatively humid year (data not shown), the seasonal course of transpiration showed a fairly constant level of maximum daily transpiration of 0.4 to 0.5 mm day^{-1} throughout summer and lasted until early autumn (JD 248, Sept. 5th) when air temperatures at night dropped close to 0 °C. Sap flux rates recovered at a lower level in a slightly warmer period in mid September but were depressed during the following frost event in a similar manner, as has been described for assimilation at alpine timberlines (Tranquillini 1979). Sap flux ceased almost completely under conditions of low light and temperatures in early October.

The spring of 1996 in the region of Zotino was dry and followed by an unusually wet summer. The growing season with noticable sap flow at the Siberian site of Bor island lasted 182 days from April 21th (day 111) to October 20th (day 293). The estimated annual transpiration of the sparse pine cover is 36.2 mm, based on 1996 and 1997 data. For 58 days (JD 225-282) in late summer the effect of different climate conditions of 1995 with a mean E_c 0.20 mm d^{-1} and the climate of 1996 with a mean E_c 0.15 mm d^{-1} shows that E_c was reduced in 1996 by 25% relative to 1995.

The response of the seasonal variation in sap flow density to available radiation air temperatures, and VPD for the second half of the summer season for two consecutive years (Fig. 8) shows the overall importance of available solar energy and the negative effect of lower temperatures (<10 °C) on tree canopy transpiration. As a result of the close correlation of radiation and VPD, the daily transpiration loss depends strongly on the daily mean irradiation. In the dry summer of 1995 the transpiration loss was more reduced at high VPD compared with the moderately humid summer of 1996.

Discussion

Xylem water flux measurements of trees, scaled up on a stand basis, provide insight into the climatic and structural limitations of transpiration. At the individual tree level, the strong effect of VPD and drought on conductance is obvious and confirms similar observations on Siberian larch (Arneth et al. 1996). In *Larix* reduced transpiration was also apparent at the leaf- (Vygodskaya et al. 1997) and at the ecosystem-level (Kelliher et al., 1996). The lack of recovery of transpiration at decreasing VPD and light in the afternoon makes it difficult to discerne the extent of diurnal reduction of conductance by stomatal closure due to high VPD from a response to water stress (Nonami, 1990; Hollinger et al. 1993).

With respect to the ecosystem water balance it seems important that canopy transpiration decreased only at high VPD in stands with high conductance and sap wood area (67 - year stand). In all other cases the decrease in conductance was compensated by an increase in VPD resulting in a more or less constant canopy transpiration over midday.

The present dataset demonstrates that there is no relation between canopy transpiration and LAI. This reduces the hope of deriving the plant water balance via remote sensing of NDVI properties (Field et al. 1994). Stand sapwood area correlated with canopy transpiration which was predicted by the pipe model (Shinozaki et al. 1964). In order to predict stand sapwood area a more detailed knowledge of stand structure is needed than presently can be derived from remote sensing. It has been shown for our stands that a good correlation exists between stem density and sapwood area which in turn results from the exponential decrease of stem number with age (self-thinning) and the linear increase of sapwood area per tree. Both processes lead to a maximum stand sapwood area during the pole stage of stand development at age 60 to 70. The stand with highest sap wood area reached transpiration rates which were by a factor of 2 higher than the average transpiration of all other stands. This result confirms the hypothesis of Grace (1993) that the hydraulic conductance of the hydroconductive system determines the rate at which forests loose water to the atmosphere.

There is an additional limitation to using remotely sensed NDVI for predicting the ecosystem water balance. In the case of the Siberian pine forest, only about 50 % of the ecosystem water loss is regulated by the tree canopy. The other half of the water loss evaporates from the understory vegetation, lichen cover, and open soil (Kelliher et al, 1998). This component of the ecosystem water balance is mainly regulated by the amount of available energy at the forest floor and by its actual water content. Tree transpiration and evaporation from the lichen layer are high after rain and decrease during dry weather. Kelliher *et al.* (1998) observed an overall correlation between soil evaporation E_u and ecosystem transpiration E_e (E_e= 0.285+0.494*E_u; r=0.83).

Based on the correlation of stand sapwood area and canopy transpiration, an improved stand classification using structural forest properties (stem density, canopy height, heartwood formation) may be derived from active microwave remote sensing with radar e.g. a combination of JERS-1 L-band and ERS-2 interferometric C-band, (Le Toan et al. 1992; Williams et al. 1995) or P-band (Rignot et al., 1995) which is sensitive to forest structures. Radar data provide seasonal information of the water status of large land surfaces, especially with respect to the freeze-thaw transitions which is important for water uptake in boreal forests (Way et al., 1997) and may provide an alternative way of functional forest classification for estimating ecosystem water loss.

For predictions of a seasonal water balance, the ratio of the average annual and summer canopy water loss is important, because in harsh environments like Siberia intensive measuring campaigns tend to focus on the summer season. Based on sap flux measurements, we predict for the 215 - year old age stand which was measured by Kelliher *et al.* (1998) a seasonal water loss of the canopy of 49 mm which is lower than the prediction of 94 mm based on summer eddy correlation measurements. The seasonal average transpiration at the 130 - year old Bor Island pine stand was 0.2 mm day^{-1}, which is almost 50% of the ten highest observed daily rates in summer (*cf.* Schulze and Hall 1982).

Using the predictions of understory transpiration of Kelliher et al. (1998) which are based on radiation at the forest floor to be 72 mm and accounting for 60 mm evaporation in summer from wet canopies, evapotranspiration during the growing season from the 215 - year old stand is estimated to be 181 mm. This is lower than the estimated by Kelliher et al. (1998) who estimated an ecosystem water loss of 265 mm by eddy correlation for the summer season from May to September with an average rainfall of 297 mm and 66 rain days. Both estimates result in a positive ecosystem water balance on an annual basis in the boreal climate of central Siberia.

The intrinsic relations between canopy conductance and assimilation (Vygodskaya et al. 1997; Wirth 1996) stress the importance of correctly predicting the water use patterns of these forests in order to quantify regional water use and gross primary productivity of the carbon cycle. The present study indicates that such predictions can be made via stand sapwood area, a parameter which can not be derived from visible/infrared range satellite remote sensing of vegetation reflective surface patterns but may be derived from remotes sensing platforms operating in the microwave range which are sensitive to vegetation structure.

Acknowledgements

The authors thank D. Wickland (NASA, Washington D.C.), B. Farmer, and D. McCleese (Jet Propulsion Laboratory, Pasadena) for supporting this study. We greatfully acknowledge the help of J.G. Goldammer, JB. Way, R. Meserth, R. Oren, B. Stumpf, N. Phillip, S. Billings and J. V. Horna during the preparation of the 1995 expedition and F. M. Kelliher and J. Lloyd for constructive critique of the manuscript. We like to thank I. Schulze, S. Grigoriyev, W. Schulze, I. Miljukova, N. Vygodskaja and D. v. Stünzner-Karbe for their help during the field work.

This research was funded by the Jet Propulsion Laboratory, California Institute of Technology, Pasadena, USA, under contract to the National Aeronautics and Space Administration (NASA), and by the Volkswagen-Stiftung I / 71846, Hannover, Germany.

References

Arneth A, Kelliher F M, Bauer G, Hollinger D Y, Byers J N, Hunt J E, McSeveny T M, Ziegler W, Vygodskaya N N, Milukova I, Sogachov A, Varlagin A, Schulze E-D (1996) Environmental regulation of xylem sap flow and total conductance of *Larix gmelinii* trees in eastern Siberia. *Tree Physiology,* **16**, 247-255.

Field CB, Gamon JA, Penuelas J (1993) Remote sensing of terrestrial photosynthesis. *Ecological Studies* Vol. 100, Springer, Berlin, pp. 511-529.

Goldammer J G, Furyaev V V (1996) *Fire in Ecosystems of Boreal Eurasia.* Kluver Academic Publishers, Dortrecht, Netherlands, 528 pp.

Granier A (1985) Une nouvelle méthode pour la mesure de flux de sève brute dans le tronc des arbres. *Annales Sciences Forestiers,* **42,** 193-200.

Grace J (1993) Consequences of xylem cavitation for plant water deficits. In: JAC Smith and H Griffiths (eds.) *Water Deficits; Plant responses from cell to community.* Bios Scientific Publishers, Oxford, pp. 109-128.

Hollinger DY, Kelliher FM, Schulze E-D, Köstner BMM (1994) Coupling tree transpiration to atmospheric turbulence. *Nature* **371,** 60-62.

Kelliher FM, Hollinger DY, Schulze E-D, Vygodskaya NN, Byers JN, Hunt JE, McSeveny TM, Milukova I, Sogachev A, Varlagin A, Ziegler W, Arneth A, Bauer G (1997) Evaporation from an eastern Siberian larch forest, *Agriculture and Forest Meteorology* **85**, 135-147.

Kelliher FM, Lloyd J, Arneth A, Byers JN, McSeveny TM, Milukova I, Grigoriev S, Panfyorov, M, Sogachev A, Varlagin A, Ziegler W, Bauer G, Schulze E-D (1998) Evaporation from a central Siberian pine forest. *Journal of Hydrology* (in press).

LeToan T, Beaudoin A, Riom J, Guyon D (1992) Relating forest biomass to SAR data. *IEEE Transactions of Geoscience and Remote Sensing,* **30**, 403 - 411.

Nonami H, Schulze E-D, Ziegler H (1990) Mechanisms of stomatal movement in response to air humidity, irradiance and xylem water potential. *Planta,* **183,** 57-64.

Phillips N, Oren R, Zimmermann R (1996) Radial patterns of xylem sap flow in non-, diffuse- and ring-porous tree species. *Plant, Cell and Environment,* **19,** 976-982.

Rignot E, Zimmermann R, Oren R, van Zyl J (1995) Spaceborne applications of P-band imaging radars for measuring forest biomass. *IEEE Transactions on Geoscience and Remote Sensing* IGARSS, Special Issue **33 (5)**, 1162 –1169.

Schulze E-D, Schulze W, Kelliher FM, Vygodskaya NN, Ziegler W, Kobak KI, Koch H, Arneth A, Kusnetsova WA, Sogatchev A, Issajev A, Bauer G, Hollinger DY (1995) Aboveground biomass and nitrogen nutrition in a chronosequence of pristine Dahurian *Larix* stands in eastern Siberia. *Canadian Journal of Forest Research*, **25**, 943-960.

Schulze E-D (1994) The regulation of plant transpiration: interactions of feedforward, feedback, and futile cycles. In: Schulze E-D (ed.) *Flux control in biological systems*. Academic Press, New York pp. 203-235.

Schulze E-D, Lange OL, Buschbom U, Kappen L, Evenari M (1972) Stomatal responses of plants growing in the desert to changes in humidity. *Planta*, **108**, 259-270.

Schulze E-D, Hall AE (1982) Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. in: *Encylopedia of Plant Physiology Vol. 12 B, Pysiological plant ecology II*, (eds. Lange O L, Nobel P S, Osmond C B, Ziegler H), Springer Verlag, Berlin, pp. 181-230.

Shinozaki K, Yoda K, Hozumi K, Kira T (1964) A quantitative analysis of plant form - the pipe model theory. II. Further evidence of the theory and its application in forest ecology. *Japanese Journal of Ecology*, **14**, 133-139.

Shvidenko A, Nilsson S (1994) What do we know about the Siberian forests? *Ambio*, **23** (7), 396-404.

Tranquillini W (1979) Physiological ecology of the alpine timberline. *Ecological Studies 32*, Springer Verlag, Berlin, 137 pp.

Vygodskaya NN, Milyukova I, Varlagin A, Tatarinov F, Sorgachov A, Kobak KI, Desyatkin R, Bauer G, Hollinger DY, Kelliher FM, Schulze ED (1997) Leaf conductance and CO_2 assimilation of *Larix gmelinii* growing in an eastern Siberian boreal forest. *Tree Physiology*, **17**, 607-615.

Walter H, Breckle S-W (1994) *Ökologie der Erde. Vol. 3: Spezielle Ökologie der gemässigten und arktischen Zonen Euro-Nordasiens*. Gustav Fischer Verlag, Stuttgart, 726 pp.

Way JB, Zimmermann R, Rignot E, McDonald KC, Oren R (1997) Winter and spring thaw as observed with imaging radar at BOREAS. *Journal of Geophysical Research* **102**, D24 29, 673-29,684.

Williams CL, McDonald KC, Rignot E, Viereck LA Way JB, Zimmermann R (1995) Monitoring, classification, and characterization of interior Alaska forests using AIRSAR and ERS-1 SAR. *Polar Record,* **31** (177), 227-234.

Wirth C (1996) *Aboveground biomass, nitrogen budget and population dynamics of a chronosequence of pine stands in Siberia.* Master thesis, University of Bayreuth, 170 pp.

Wirth C, Schulze E-D, Vygodskaya NN, Ziegler W, v.Stünzner-Karbe D, Schulze W, Milukova I, Sogachev A, Varlagin A, Zimmermann R, Panvyorov M, Backor M, Grigoriev S, Kusnetzova W (1998) Aboveground biomass, structure and self-thinning of pristine Scots pine forests in Siberia as controlled by competition and fire. *Oecologia* (Berl.), (submitted).

Wismann V, Cavanie A, Hoekman D, Woodhouse I, Boehnke K, Schmullius C (1996) Land surface Observations using the ERS-1 Windscatterometer. *European Space Agency,* Final Report #11103/94/NL/CN, University of Wageningen, Netherlands, 57 pp.

Tables

Average tree age (years)	Range of tree age (years)	Canopy height (sd) (m)	Stand density (trees m^{-2})	DBH (sd) (m)	Above-ground Biomass (kg m^{-2})	Basal Area ($m^2 m^{-2}$)	Leaf Area Index ($m^2 m^{-2}$)	Sapwood Area ($m^2 m^{-2}$)
28	28	3.4 (1.1)	0.94	0.03 (0.014)	1.509	0.000719	0.55	0.000472
66	65...67	10.5 (1.6)	0.28	0.10 (0.026)	7.281	0.002740	1.55	0.001141
202.6	201...204	16.3 (2.1)	0.08	0.22 (0.056)	10.424	0.002890	1.45	0.000769
383.2	380...387	19.5 (2.3)	0.046	0.33 (0.058)	14.084	0.003350	1.60	0.000680
242.8	140...430	14.6 (4.6)	0.023	0.26 (0.117)	6.036	0.001340	0.60	0.000372

Table 1: Stand parameters for a chronosequence of *Pinus sylvestris L.* stands in Central Siberia. Location at 60° 44' North, 89° 08' East, elevation 100-105 m a.s.l. Leaf area was calculated from biometric harvest. Data from Wirth (1996).

Figure Legends

Figure 1: Transects along a chronosequence of pristine, mesic *Pinus sylvestris* L. stands west of the Yenisei River, Central Siberia. The stands from 28 - year old to 383 - year old are homogeneous in age and structure. The multi-cohort 140 to 430 - year old stand represents a heterogenous stand structure. Modified after Wirth (1996).

Figure 2: Daily mean (T_{av}, diamonds, top), maximum (T_{max}, filled circles, top) and minimum (T_{min}, open circles, top) air temperature, daily maximum (VPD_{max}, open squares, bottom) and mean (VPD_m, open circles, bottom) vapor pressure deficit (VPD), and daily sum of precipitation (P, filled bars, bottom) for 11 days in August 1995 at Bor Island near Zotino, Central Siberia. The peri-glacial sand dune of Bor Island is covered with a 130 - year old *Pinus sylvestris* L. stand and completely surrounded by shallow *Sphagnum* bogs. Minimum, average and maximum values of air temperature and VPD represent the mean of 10 min intervals, measured every 30 seconds.

Figure 3: Daily course of tree xylem sap flux density measured on individual stems of *Pinus sylvestris* L. in five forest stands along a chronosequence of Scots pine near Zotino, Central Siberia. Symbols show sap flux density in individual trees within each stand ($g_{H2O}\ m^{-2}{}_{sapwood\ area}\ s^{-1}$) measured from 0 to 20 mm depth relative to the cambium. Values shown represent means of 20 -

minute time intervals, measured every 30 seconds. The day shown (August 7th, 1995) is in the middle of the dry period when VPD reached 2.7 kPa at 20 °C air temperature and maximum topsoil temperatures were 25 °C in closed canopy stands and up to 35 °C in open stands. Within each plot diurnal flow patterns were relatively uniform and independent of tree size. Only suppressed and damaged trees had lower flux rates while emergent trees tended to show higher rates than the canopy average. The daily course of sap flow density was distinct for each stand age class. Trees of the 28 - year old stand reached the highest sap flux density as compared to all other plots. With increasing stand age, the variation in sap flow rates between trees in the same stand increased due to the individual history of crown and stem damage.

Figure 4: Daily sums and variance of tree canopy transpiration (top) and daily mean tree canopy conductance and variance for water vapor (bottom) for a chronosequence of five *Pinus sylvestris* L. stands near Zotino, Central Siberia in August 1995. Canopy transpiration and canopy conductance were calculated from the average sap flux of measured trees (n=7 to 9 per stand) and the total stand sap wood area. The 28 -year old stand (filled squares) was measured on days 219 and 220. The measurements were made during a period of warm and dry weather between two major rain events. Canopy conductance was high after rainfall (day 215) and decreased continuously in all age classes to a lower and constant level within 4 to 5 days. Transpiration remained at a relatively constant level for all sites with exception of the 67 - year old stand.

Figure 5: Daily sums and variance of tree canopy transpiration (top) and daily mean tree canopy conductance and variance for water vapor (bottom) in relation to the daily mean vapor pressure deficit for a chronosequence of five *Pinus sylvestris* L. stands near Zotino, Central Siberia in August 1995. The 28 - year old stand (filled squares) was measured on days 219 and 220. The canopy conductance showed pronounced stomatal closure from at a high level in the 67 - year old pole stand which lead to a decreased transpiration at high VPD. In all other stands the change in conductance did not significantly reduce the water loss by transpiration.

Figure 6: Tree density (D), leaf area index (LAI), tree canopy transpiration (E_c), stand sapwood area (SA), and the ratio of stand sapwood area / stem density (SAD) in relation to the average stand age of a chronosequence of five *Pinus sylvestris* L. stands near Zotino, Central Siberia. Biometric data from Wirth (1996). Tree density decreased with stand age and sapwood area per tree increased almost linearly, resulting in a maximum stand sapwood area in dense pole stands before self- thinning becomes prevalent. Canopy transpiration was not related to LAI or to stand basal area but closely correlated with stand sapwood area (E= -0.02 + 1.15 SA, r=0.96).

Figure 7: Annual course of daily sum of photon flux (top), mean daily air temperature (open circles, middle), mean daily vapor pressure deficit (open bars, middle) and daily sum of tree canopy transpiration (bottom) for days from 1996 to 1997 (large box, left) and 1995 (small box, right) at Bor Island near

Zotino, Central Siberia. The seasonal course (large box, left) results from combined measurements of the years 1996 (days 202-366) and 1997 (days 1-163) since frost and bear damages interrupted the measurements twice at the remote location. The growing season with noticable sap flow lasted 182 days from April 21th (day 111) to October 20th (day 293). The estimated annual transpiration of the sparse pine cover on the island is 36.2 mm. For 58 days (days 225-282) in late summer the effect of different climate conditions of 1995 with a mean E_c 0.20 mm d^{-1} and the climate of 1996 with a mean E_c 0.15 mm d^{-1} shows that E_c was reduced in 1996 by 25 % relative to 1995.

Figure 8: Daily sum of tree canopy transpiration in relation to daily sum of photon radiation (left), mean air temperature (center), and mean daily vapor pressure deficit (left) for a 130 - year old *Pinus sylvestris* L. stand at Bor Island near Zotino, Central Siberia. Data are shown for August 13th - October 9th for the two consecutive years of 1995 with a dry summer (open circles) and 1996 with a wet summer (filled circles). As a result of the close correlation of radiation and VPD, the daily canopy transpiration loss depends strongly on the daily mean irradiation. In the dry summer of 1995 the transpiration loss was more reduced at high VPD compared with the moderately humid summer of 1996.

Figures

Figure 1

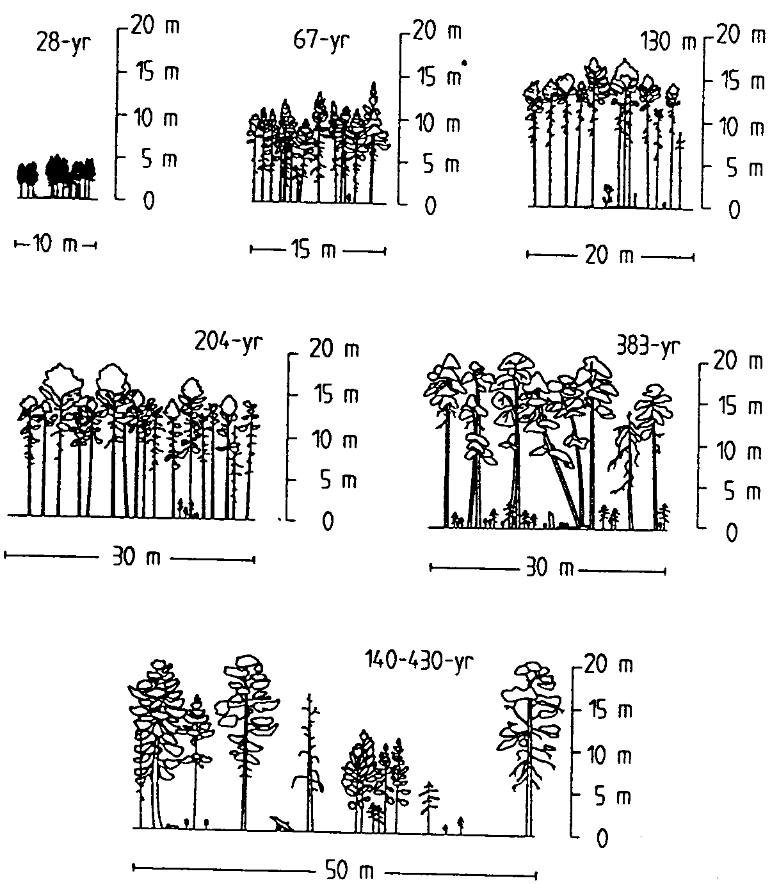


Figure 2

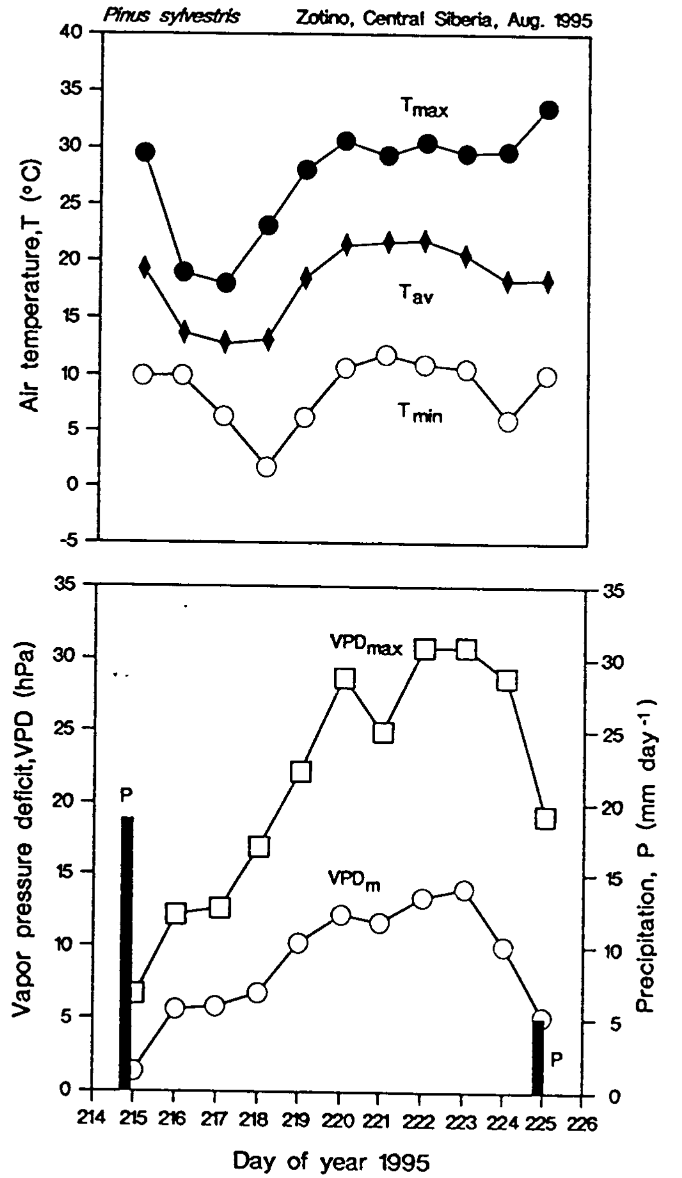


Figure 3

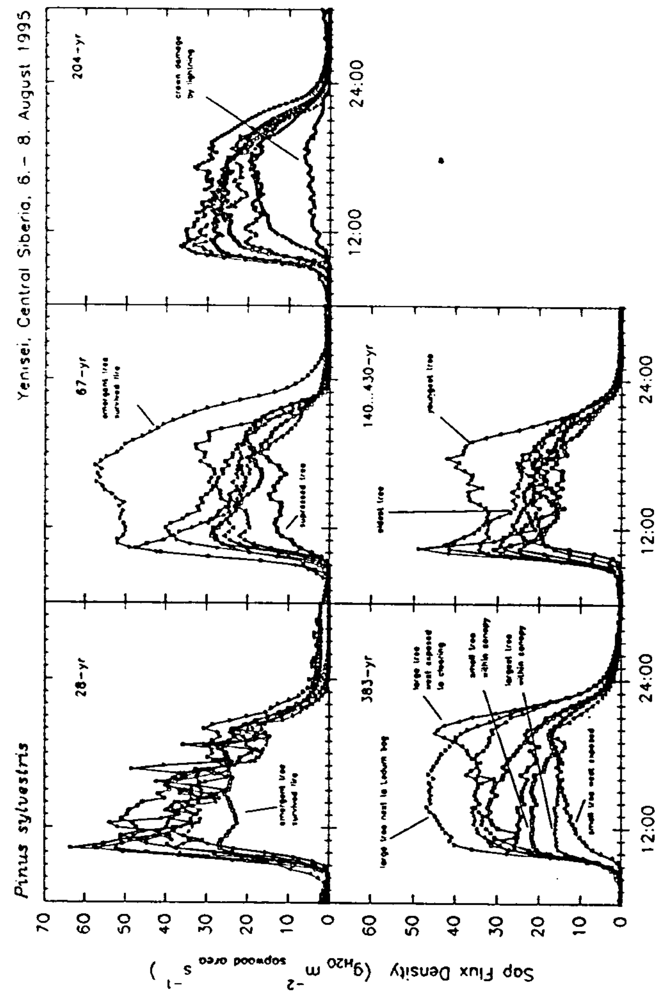


Figure 4

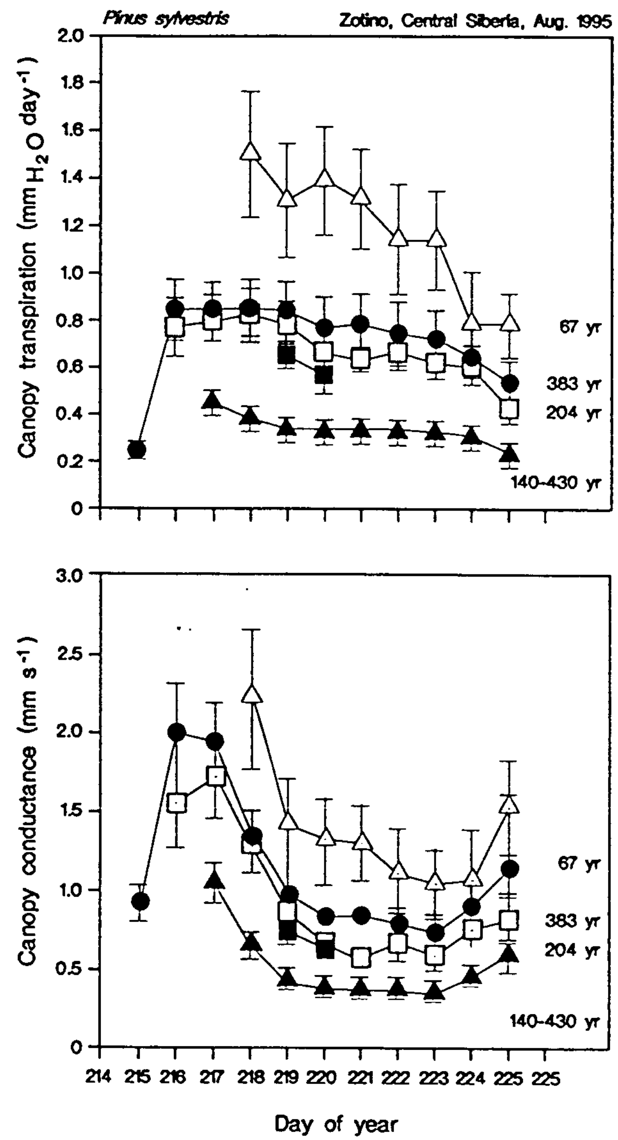


Figure 5

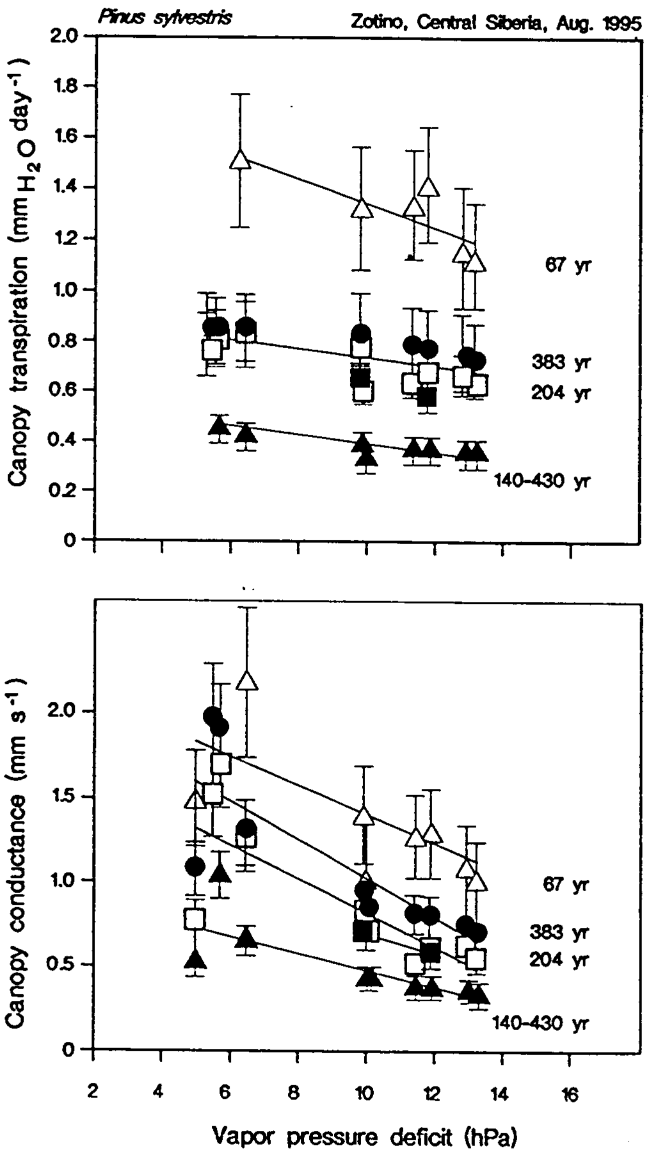
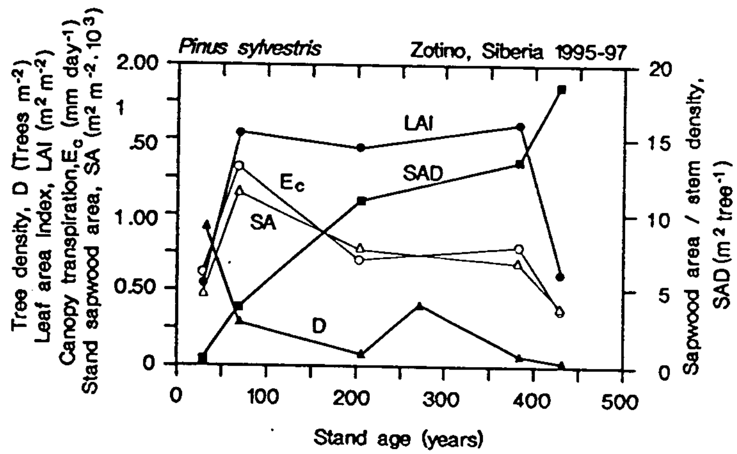
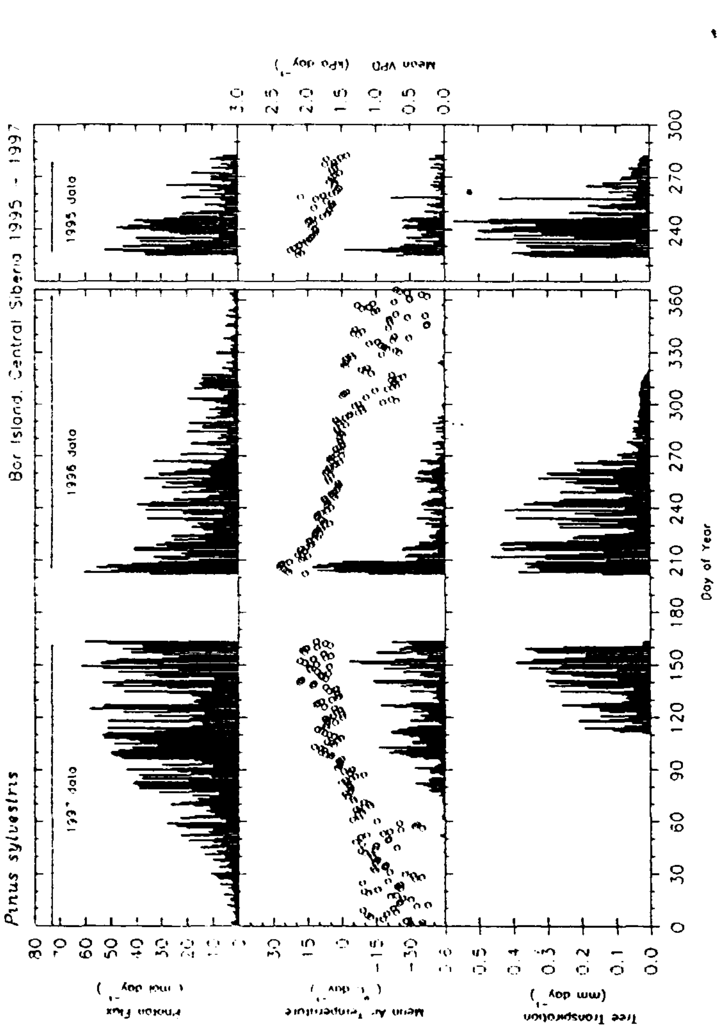


Figure 6




Pinus sylvestris
Bor Island, Central Siberia 1995 - 1997
1995 data
1996 data
Photon Flux
Mean Air Temperature
Tree Transpiration (mm day⁻¹)
Mean VPD (kPa day⁻¹)
Day of Year

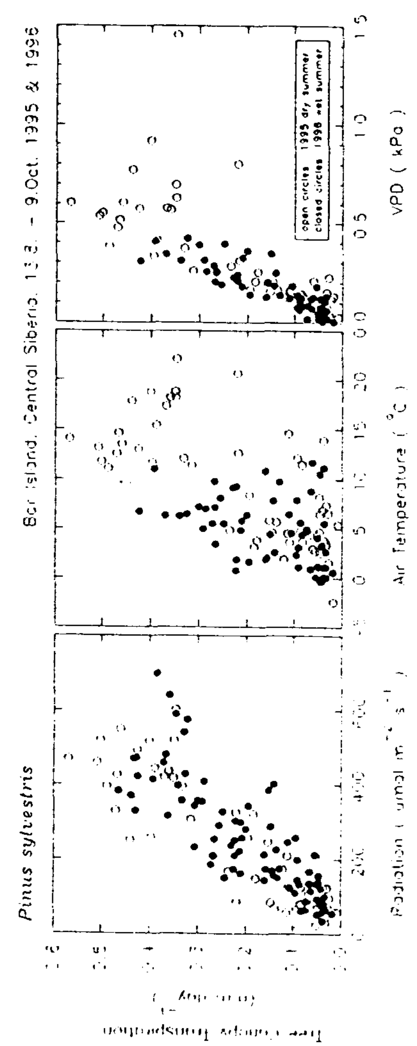

Pinus sylvestris
Bor Island, Central Siberia
open circles 1995 dry summer
closed circles 1996 wet summer
Tree canopy Transpiration
Air Temperature (°C)
VPD (kPa)

Figure 8